

**ARMAMENTS AND ORNAMENTS:
MATE-GUARDING AND THE EVOLUTIONARY ROOTS OF RELIGION**

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Abstract

This article explores the connection between sexual selection and religion, locating the origins of religious behavior in mate guarding after the transition to terrestrial life in *Homo erectus* 1.8 million years ago. An important consequence of the transition was the emergence of a polygynous, multiple-family social structure, which gave rise to mate guarding as a successful strategy. Further, as a result of sleeping on the ground, REM (rapid-eye-movement) phases were substantially extended. This produced novel dream experiences in *Homo erectus*, which is identified as the origin of proto-religious traits. The article argues that proto-religious dream experiences and related behavioral expressions gave males psychological and strategic advantages in keeping competitors away from their females. Given the strong selective pressure of male competition in polygynous mating systems, biological traits underlying proto-religion were successful in natural selection. Finally, it is suggested how subsequent evolutionary leaps in human cognition shaped religious thought and behavior and their role in sexual selection. The article is concluded by outlining how elements of the mate-guarding hypothesis could be tested and improved using empirical methods.

Keywords

origins of religion; sexual selection; mate guarding; terrestrial life; ground sleep; dreams; *Homo erectus*

Introduction

Sexual selection is a powerful process of evolutionary change, the effects of which on religion have received relatively little attention so far. Scholars who commented on the subject (see below) mainly focused on the effects of mating preferences (mate choice) in men and women, with particular attention to female choice. In this article I will draw on recent insights about human sexual selection and argue that male contest played a pivotal role in the early development of human religion. I will pinpoint the move to a fully terrestrial life in *Homo erectus* about 1.8 million years ago as the decisive moment for the appearance of proto-religious traits. Two implications of this change in lifestyle will be examined, in particular: first, the emergence of a polygynous, multiple-family social structure; second, the appearance of extended REM (rapid-eye-movement) sleep as a result of sleep on the ground. I will argue that mate guarding provided the selective force responsible for the spread of archaic religious thought and behavior. Male intra-sexual competition, as it will become clear, is capable of producing stronger selection than any other form of evolution, which accounts for the perseverance and strong motivational power of religion in all known human societies past and present.

What is Sexual Selection?

While some scholars treat sexual selection as a special case of natural selection (Clutton-Brock, 2004), others (following Darwin) consider it a different type of evolutionary process (Safran, Scordato, Symes, Rodríguez, & Mendelson, 2013). In

fact, sexual selection improves mating success and partner choice at the cost of other components of reproductive success, such as adult survival (Stearns & Hoekstra, 2005, pp. 249–251). A trait variant that helps the organism to produce more offspring with partners of better quality (see below) will spread as long as its possible negative effects on other aspects of reproductive success (such as preventing the organism from reaching reproductive age or raising the offspring) do not outweigh its advantages. Sexual selection is an extremely strong and rapid evolutionary process. Darwin's observations about the often dramatic differences between males of closely related biological taxa as well as between males of the same species lead him to the concept of sexual selection (Darwin, 1909, pp. 166–168).

The *operational sex ratio* is the ratio of sexually active males and receptive females at a given time (Clutton-Brock & Vincent, 1991; Clutton-Brock, 1991; Kvarnemo, Ahnesjö, & Ahnesjö, 1996). The sex that is in excess in terms of operational sex ratio will predominantly compete for access to mating partners and will undergo stronger sexual selection. An important component of the operational sex ratio is the difference between the potential reproductive rates of the sexes. The *potential reproductive rate* is the maximum number of offspring that parents can produce independently in a unit time if there is no limitation on the number of mating partners. Although males typically have higher potential reproductive rates, environmental factors (such as temperature, food and the availability of nest site) can influence the potential reproductive rates of the sexes differently, changing and even reversing the operational sex ratio. This can result in reverse sex roles and temporary switches of sex roles in species. Various other factors can influence the operational sex ratio (Stearns & Hoekstra, 2005, pp. 265–266): how females form groups; the differences between the sexes in terms of survival rates; and the time each sex invests into finding mating

partners, breeding, and caring for the offspring. In the context of primate and hominid sexual selection, differences in parental investment influence sexual selection significantly (Trivers, 1972). The biological costs of pregnancy and lactation for females are far greater than the cost of producing sperm and copulating, which is the typical investment of male primates. The contribution of males to parenting varied in hominid evolution, which we will consider later.

The reason for the power of sexual selection, observed by Darwin, is that it can cause large variation in lifetime reproductive success. In addition to the operational sex ratio, the strength of sexual selection is influenced by the *variation in the number of mates* per male (Shuster & Wade, 2003). If males compete for mating, any successful mating for one male is a missed opportunity for another male. Thus lifetime reproductive success varies more for males than for females, resulting in a stronger selection of sexually selected traits in males than of other traits in either males or females. The variation in the number of mates per male depends on the spatial and temporal aggregation of females and on female life history. For example, if females are aggregated in groups, a successful male can mate with many females while other males with none, which increases the variation in mating success. A male can defend an aggregated group of females, preventing mating between females in the harem and other males, a possibility that will be of special interest for the argument of the present article. If females are sexually receptive simultaneously then members of the other sex have a more difficult time monopolizing them. Finally, if females are polyandric (mate with different males) and have several sets of offspring in a lifetime, the chances of males to level out differences in mating opportunities increases and variation in male reproductive success decreases.

The traits selected for in sexual selection are often described as “armaments and ornaments” (Berglund, Bisazza, & Pilastro, 1996). *Armaments* evolve because they increase success in the intra-sexual competition for mating with members of the limiting sex. *Ornaments*, in turn, serve as clues for the limiting sex as they chose mating partners. It is important to note that choice does not require any conscious deliberation and decision-making, even if we speak of human sexual selection. It is best to think of mate choice as a signaling system relying on evolved signal sending and receiving mechanisms. In fact, the perception of the limiting sex constitutes an important constraint for the evolution of ornaments. It has been suggested that the co-evolution of ornaments in one sex and a corresponding preference for the ornaments in the opposite sex can result in rapid, runaway selection (Stearns & Hoekstra, 2005, pp. 260–261).

In addition to intra-sexual contest and mate choice, the third arena of sexual selection is *intersexual conflict*. This conflict arises from the fact that optimal outcomes for the two sexes require different mating strategies (Kappeler & van Schaik, 2004; Watson-Capps, 2009). In humans (and most primates), intersexual conflict manifests itself as male sexual coercion (using harassment, exchange, or rape) and infanticide (killing competitors’ offspring), as well as counter-measures by females, such as physical avoidance and resistance, female bonding, seeking protection from male “body-guards,” confusing paternity (to minimize infanticide), and the synchronization of reproductive cycles (so that it is more difficult for a single male to monopolize females). An important consequence of sexual conflict is the female tendency to combine protection by a long-term partner (seeking immediate benefits over good genes) while using opportunities for mating with other males (looking for good genes rather than reliable partners).

Religion and Sexual Selection: The Emphasis on Female Choice

There can be two main reasons for choosing a mating partner in the framework on sexual selection: for immediate benefits (such as providing protection or food) or for good genes (that contribute to the fitness of the common offspring). However, good genes, health, and the lack of parasites are difficult to assess by potential mates. Biological ornaments (the textbook example being the peacock's tail), behavioral displays (such as courtship dances), or artifacts (such as the bowerbird's nest) could function as signals of good genes. They can be seen as "handicaps" (Zahavi & Zahavi, 1997), for example, by attracting predators, slowing down the organism's movement, or draining other important resources. Sexually selected ornaments are costly and hard-to-fake signals of the potential mate's quality: the more fitness the organism has, the more of such luxuries it can afford.

In the human species, the female sex is the limiting sex for reproduction, as women invest substantially more time into reproduction (including pregnancy, giving birth, and breast-feeding) and in any society there will be less receptive women than sexually active men, at most times. Men are thus expected to compete for mating partners, whereas women are expected to choose from potential mating partner. Geoffrey Miller (1993, 1999) suggested that human courtship, and women's mating choice, in particular, explains various aspects of culture. Miller noted the tendency for men to produce more extravagant displays of intelligence and courage: "[m]ale humans paint more pictures, record more jazz albums, write more books, commit more murders, and perform more strange feats to enter the Guinness Book" (Miller, 2001, p. 82). A possible explanation for the tendency among young males to show off their intellectual

prowess more eagerly than do women, Miller (1993) suggested, is runaway sexual selection. According to the theory of (Fisherian) runaway selection, (male) sexual ornaments co-evolve with (female) preferences for them, potentially resulting in rapid evolutionary change.

In his more recent work, Miller (2001, 2007) focused on both male and female choice. Among our human ancestors living in the Pleistocene (between 1.6 million and 10 thousand years ago), Miller argued, both men and women favored partners who “showed taste and talent in their everyday self-ornamentation over those who did not, all else being equal” (Miller, 2001, p. 274). These displays were reliable indicators of fitness, since “beauty equals difficulty and high cost”: things that are attractive “could have been produced only by people with attractive, high-fitness qualities such as health, energy, endurance, hand-eye coordination, fine motor control, intelligence, creativity, access to rare materials, the ability to learn difficult skills, and lots of free time” (Miller, 2001, p. 281). By a similar argument, Miller (2007) proposed that moral virtues, such as kindness, empathy, niceness, honesty, and heroism, were also selected by mate choice.

Following the line of reasoning set out by Miller, scholars put forward explanations of various aspects of religion in terms of sexual selection. Slone et al. (2008) proposed that religions evolved, at least in part, to support the assessment of the qualities of potential mates. Pyysiäinen (2009, pp. 207–208) proposed that ritual dance can be a good indicator of male fitness and thus function as a male ornament in sexual selection. More generally, Pyysiäinen suggested that religion could be a good indicator of fitness because

[1] it becomes important in puberty (rites of initiation); [2] it is male-dominated (women mostly are “audience”); [3] it is costly in terms of time and resources (the handicap principle); [4] it is species-specific, like all sexually selected traits; [5] there are heritable differences in “religious” attitudes and behavior (...); and [6] “religion” has a multimodular basis in mind. (Pyysiäinen, 2009, p. 209)

Elaborating on previous discussions, Pyysiäinen (2009, pp. 208–209) also suggested that celibacy could be an answer to the problem of males who could not find mating opportunities. Turning to the model of kin-selection, Pyysiäinen concluded that celibate individuals help the survival of their genes by helping close relatives.

Vaas and Blume (2009, pp. 136–137) observed that more men than women practice religion in the public and most new religious movements and sects have male founders, despite the fact that more women than men have a personal appreciation for religiosity, spirituality, and esotericism. They identified the following elements of religion, in which typically males engage themselves, as potential hard-to-fake signals of fitness: tortures of the body; time-consuming rituals (rosary, processions); postures that prevent other actions (crossed arms, deep bows); life-long scriptural studies, meditations, prayers; renouncing consume or nourishment (fasting); high costs of temples, costumes, and art.

Also inspired by Miller’s hypothesis, Martin (2013, pp. 197–198) proposed that religious storytelling could be an effective form of courtship. Referring to Boyer’s (1994, 2002) theory of the success of minimally counterintuitive ideas in cultural transmission, Martin asks why people would be motivated to entertain minimally counterintuitive ideas in first place. He goes on proposing that the ambition to be an

innovative storyteller (and thereby attract mating partners) could provide the intentional motivation for constructing the ontological violations that are described by Boyer's theory.

If the mating system includes long-term bonding between males and females, female choice can target benefits such as giving protection and providing food (in addition to looking for good genes and health). Vaas and Blume (2009, pp. 137–138) suggested that religious commitment can function as a proxy for marital faithfulness. According to Sommer (2000b, pp. 165–182), in the hunter-gatherer tribes of the Pleistocene women performed rituals (with menstrual symbolism) to deter opportunist mating attempts when the fittest men were away on hunting expeditions. To the extent that men invest into long-term partnership (and participate in childcare), male choice for female faithfulness also becomes relevant. While motherhood (at least from the mother's perspective) is always certain, fatherhood is (historically) uncertain. In addition to serving female choice (reproducing with good hunters), this arrangement also encourages hunters to provide food by ensuring them that they provide for their own offspring. Deacon (1997, p. 408) proposed that ceremonial marriage among hunter-gatherers served exactly the latter purpose.

Some ethnographic and experimental data suggests that religious beliefs and behavior support long-term, monogamous relationships at least in some contemporary societies. Experiments and surveys (Bulbulia et al., 2015; McCullough & Willoughby, 2009; Weeden, Cohen, & Kenrick, 2008; Van Slyke 2015; Weeden 2015) lead to the conclusion that religious participation helps monogamous, high-fertility reproductive strategies by promoting marital commitment in both men and women. Nesse (2001, pp. 304–305) hypothesized that religion can work as a signal for both sexes, depending on particular social circumstances: men on the island of Utila use women's religious

displays to predict marital faithfulness, whereas men among the Yomut in northern Iran (who tend to spend time away from their families) are more religious than women to signal marital commitments. Finally, some studies (Li, Cohen, Weeden, & Kenrick, 2010; Blume 2015) found that exposure to the image of attractive members of the same sex increases self-reported religiosity in both women and men. This result can be used to support a view of religion as both ornament (attractive trait) and armament (a trait that helps fighting off competition).

As it became evident from our short survey, most research on religion and sexual selection concentrated on mate choice, in general, or female choice, in particular, more or less along the lines of Miller's work. Among the few studies that explored other perspectives, we can mention Palmer and Begley's (2015) discussion of parental influence, who suggested that the explanation of religion has to consider the role of religious traditions in encouraging cooperation between relatives, which they understand in the framework of inclusive fitness. Sela, Shackelford, and Liddle (2015) made a case for the use of religion as a tool of aggression in sexual selection. They noted that both intrasexual aggression between men and various forms of intersexual aggression by men toward women provide males with a reproductive advantage. They cited examples from (Abrahamic) religious traditions to show how religion contributes to mate guarding. Pazhoohi et al. (2017) suggested that religious veiling is a mate-guarding strategy and showed that the practice becomes more frequent in harsher environments. They hypothesized that this was explained by the higher involvement of fathers in parenting in harsh environments than in less demanding ones, although they noted that wearing more clothing in harsher environments for protection from the weather is a possible alternative explanation.

Is Mate Choice the Way to Go?

We have seen that most theorizing about the connection between sexual selection and religion focused on female choice. In this section, I will review recent ethnographic, anatomical, and genetic studies to see if that approach is justified.

The ethnographic evidence

Let us start with the ethnographic evidence. Apostolou (2007a) used Murdock's *Ethnographic Atlas* (Murdock, 1967) to analyze the marriage patterns of all 190 modern-day hunter and gatherer societies for which sufficient data existed. Marriage (which is considered a universal institution) was found in all societies in the study. In 69.9% of hunter and gatherer societies studied, marriage is predominantly based on parental arrangement, whereas in another 17.7% it is based on arrangement by close kin. Courtship subject to parental approval is the rule in further 8.1% of societies, whereas courtship is the primary form of marriage in only 4.3%. When marriage is arranged, the decision typically lies with male relatives (father, brothers of the bride, and her uncles), although the informal role played by female relatives could be significant. Apostolou (2007a, p. 405) also found that as many as 73.7% of all the hunter-gatherers in his study practiced polygyny, usually reported to be the privilege of a few men. Based on these results, Apostolou (2014) suggests that parental choice rather than female choice should be considered as the driving force of sexual selection in Pleistocene human societies, followed by male-male competition and female choice. While the criteria for mate choice and parental choice overlap to some extent, the difference in the genetic contribution of an individual to a child versus a grandchild

changes the relative importance of traits when choosing a spouse or an in-law, respectively (Apostolou 2007b; 2014, with further references).

Walker and colleagues (Walker, Hill, Flinn, & Ellsworth, 2011) used genetic information from surviving hunter and gatherer societies about which data regarding marriage is available. They reconstructed a phylogenetic tree of the societies and calculated the most probable ancestral form of marriage. Their model predicts that humans leaving Africa about 50,000 years ago practiced arranged marriage. The study is inconclusive about earlier societies, since courtship is found in many contemporary African hunter-gatherers. The study found no correlation between environmental factors and marriage types, confirming the conservative nature of marriage systems. Walker and colleagues (2011, p. 4) suggest that external pressures are more likely to lead to the gradual deregulation of marriage (thus the later appearance of courtship, perhaps influenced by Bantu expansion in Africa) than to stronger regulation.

In light of the evidence presented in these studies, it seems difficult to maintain Miller's position (see above) that courtship and female choice have been the dominant force of sexual selection in human pre-history. Further, the widespread notion (e.g., Sommer, 2000a) that patriarchal structures were introduced into human societies after the advent of agriculture (that is, about 10,000 years ago) is called into question. However, when considering the evolution of our species (for example, since our separation from our chimpanzee cousins about 6 million years ago), the study of conditions that prevailed a few thousand years ago barely scratches the surface. Since Walker and colleagues' study is inconclusive with regard to the mating system of humans earlier than 50,000 years ago (although providing strong arguments for arranged marriage being the ancestral condition), we have to consider different types of data.

The anatomical evidence

Let us now turn to arguments based on anatomical evidence. Courtship and female choice in birds fascinated Darwin and still fascinates many modern scholars, providing inspiration for understanding human mating behavior. Across bird species, one finds strong female choice (resulting in spectacular male ornaments and elaborate courtship), polyandry (resulting in ornamented females), and complex mating systems where both males and females can practice monogamy and polygamy (Clutton-Brock, 2007; Stearns & Hoekstra, 2005, pp. 266–269). Puts (2010) observes that same-sex contest (typically between males) can override other forms of sexual selection (such as mate choice and sperm competition). If a male can win contests definitely and exclude other males from mating with certain females there is no room for female choice. If mating opportunities still remain open for the losers, female choice can take place. Puts then examines the factors that determine the strength of male-male contest. The dimensionality of the mating environment forms a general constraint: it is easier to observe and deter competitors in two-dimensional space (on solid ground) than in three-dimensional spaces (such as deep water, arboreal habitat, or the air). For example, elephant seals can keep harems because they mate on shore, whereas Weddel seals mating under water cannot. Ecological constraints (of body mass) also prevent most birds and arboreal animals from evolving toward strong contest: bird species where contest is strong are typically terrestrial. Anatomy reveals much about sexual selection for contest: as body-mass grows, the force of blows increases more rapidly than defensive ability, making competition more likely in large animals.

With regard to humans, Puts (2010, pp. 161–163) observes that the modest dimorphism in the overall body mass of men and women is misleading, because women

have fat deposits that are unique among apes. When considering fat-free body mass, men are 40% heavier than women. Men also have 80% more arm muscle mass than women and the sex difference in upper-body muscle mass is similar to that among gorillas. Sex differences in strength, vertical leap, and sprint times are considerable. Both boys and men are much more aggressive than women and male aggression shows positive correlation with dominance. Men have cognitive adaptations for using projectile weapons (which constitutes the largest known cognitive sex difference), the use of which for warfare rather than hunting is suggested by men's superior intercepting abilities.¹ These male characteristics suggest high male competition in our ancestors. Since the female body does not reveal when women are fertile, contest among men was likely to be for dominance and not for short-term victories (p. 164). Finally, Puts (2010, p. 166) suggests that whereas some signs of masculinity (muscular build, deep voice) are sexually attractive, others (such as beard and thick eyebrows) are not or not consistently. All of these features, however, are effective signals of dominance and have a stronger effect on dominance (as perceived by other men) than on sexual attractiveness (even near ovulation, when women typically favor masculinity). Puts concludes (2010, p. 163) that the most plausible ancestral mating system was the control of females by a group of males, who both competed aggressively with other groups and maintained a hierarchy of dominance among each other.

Dixson (2009, pp. 124–154) offers a comprehensive analysis of human sexual dimorphism against the background of sexual dimorphism in other primates. In particular, Dixson asks if human morphological traits are consistent with a monogamous, polygynous, or multiple-male/multiple-female mating system. Body

¹ Puts' claim about male adaptations to use projectiles could be reformulated more carefully: there are observed biases in spatial cognition that lend themselves to such interpretation. For the hypothesis of the use of projectiles as a male adaptation for warfare, see recently Lombardo & Deaner, 2018.

size, muscle mass, and strength, together with arguments presented elsewhere in the book, point to a polygynous mating system with two to three females per male. Dixon dedicates an entire chapter (2009, pp. 168–186) to the debate on sperm-competition, concluding that it is limited humans, which is consistent with polygyny as an ancestral condition. A high level of sperm-competition (e.g., Pham & Shackelford, 2014; Shackelford & Goetz, 2007), in contrast, would indicate a multiple-male/multiple-female mating system. The strongest argument against high sperm-competition is the small testicle size of humans relative to that of chimpanzees and bonobos. The shape of human sperm is another piece of evidence pointing in the same direction. Numerous other aspects of the debate (such as penile morphology, female orgasm, oviductal length, and copulatory patterns) are reviewed by Dixon; without rehearsing the entire discussion, I am going to accept his results at this place. Bimaturism (boys maturing later than girls) and differences in lifespan support this conclusion. The late maturity of males in sexually dimorphic apes and monkeys as well as the shorter lifespan of males in a variety of mammal and bird species are understood to result from inter-male competition. The size of heart and lungs, together with a higher number of red blood cells and higher concentration of haemoglobin (all considered as adaptations for hunting, fighting, and manipulating heavy objects), as well as female fat deposits (adaptations for pregnancy and lactation), also indicate polygyny. Dixon suggests, however, that female choice influenced various physical male traits in humans as well as male choice played a role in women's lighter skin and waistline. When it comes to dimorphism in facial characteristics, Dixon identifies clues of both polygynous and monogamous mating systems in human precursors, but on balance concludes that the visual characteristics of adult male facial hair and baldness (together with body hair) suggest high sexual dimorphism and polygyny (Dixon, 2009, p. 149).

Yet another possibility to use anatomy for assessing male-male competition in ancestral populations is measuring the ratio of the second and fourth digits of the male hand, also called the 2D:4D ratio. Although the exact mechanism behind the ratio has not been established conclusively (exposure to androgen in the womb being the generally supported idea), it has been reliably demonstrated that a lower 2D:4D ratio in men is associated with a higher level of aggression (Bailey & Hurd, 2005; Manning & Fink, 2018). For example, soccer players of a club who were given one or more red cards during a season (meaning that they committed serious or repeated foul play in one or two games) exhibited lower 2D:4D ratios than other players (Mailhos et al., 2016). It can be argued that testosterone favors or promotes the development of masculine attributes, many of which are associated with male-male competition. Thus 2D:4D ratio can be seen as an additional sexual dimorphism, associated with other attributes relevant for competition. Nelson and colleagues (Nelson, Rolian, Cashmore, & Shultz, 2011) analyzed 2D:4D data collected from modern humans as well as from living and extinct hominid species. When analyzing the archeological evidence, the method involved measuring the first (proximate) phalanx of the fingers (2PP:4PP), which is best preserved. Using the correlation between 2D:4D ratio and mating systems in living species as a benchmark, Nelson and colleagues concluded that both contemporary humans and *Australopithecus afarensis* (our hominid ancestor that lived 3.9–2.9 million years ago, made famous by “Lucy”) are somewhere between monogamous gibbons and polygynous apes. The mating system of more distant hominid relatives (*Ardipithecus*, *Hispanopithecus*, *Pierolapithecus*), as shown by the model, was polygynous. Most importantly, however, the anatomically modern human who lived in the Levant 90,000 years ago (attested by remains from the cave Qafzeh 9) is categorized as polygynous, together with the majority of Neanderthals. The authors

suggest (Nelson et al., p. 1561) that the social system of our Middle and Late Pleistocene ancestors was “more promiscuous” than that of most contemporary human populations.

We can add that *Australopithecus afarensis* is well-represented in the fossil record and the overwhelming majority of studies that are based on a wider range of characteristics (not only 2D:4D ratio) concluded that this species had high sexual dimorphism, approaching or even exceeding that of gorillas (Plavcan, 2012, pp. 49–50). Other *australopithecines* also show high dimorphism in general, although this can vary across anatomical traits (Plavcan, 2012, p. 50). Interestingly, notwithstanding the conclusions of the 2D:4D analysis, another study (White et al., 2009) based on other skeletal and dental material found little evidence of dimorphism in *Ardipithecus*. This species was our ancestor, or possibly cousin, that lived before *Australopithecus*, but after the separation from a common ancestor shared with chimpanzees and bonobos. Finally, Plavcan (2012), who offers a thorough discussion of the material as well as insights about the connection between different aspects of dimorphism and ecological factors, suggests (pp. 58–60) that the most parsimonious hypothesis is that the last common ancestor of humans and chimpanzees had chimpanzee-like sexual dimorphism. He adds that dimorphism could fluctuate due to ecological constraints (for example, females of a species getting bigger synchronously with males and becoming more slender again as ecological costs arose) and warns that while high dimorphism indicates male mate competition, low dimorphism does not necessarily indicate a lack thereof.

The genetic evidence

The last type of evidence comes from the analysis of molecular genetic data derived from living human populations. Dupanloup and colleagues (2003) analyzed data from the Y chromosome of men from all continents to calculate how male population grew in the past of humankind. Population changes such as migration, geographic dispersal, admixture, and rapid changes in population size can be inferred from the analysis of non-recombining DNA.² Dupanloup and colleagues found a mismatch between the previously established expansion of the female population (based on mitochondrial DNA), on the one hand, and the expansion of the male population calculated from the Y chromosomes. The only reasonable explanation they could find for the difference is that the male population underwent rapid growth relatively recently. This is only possible, they argue, if less men than women contributed to reproduction; in other words, the *effective population size* of males had been low until 10,000 years ago. The most straightforward conclusion is that a shift from polygyny to monogamy occurred at that time. In a more recent study, Labuda and colleagues (Labuda, Lefebvre, Nadeau, & Roy-Gagnon, 2010) analyzed data from West African, Western European, and Chinese populations. They calculated a breeding ratio of women to men of 1.42 in West Africa, 1.34 in Western Europe, and 1.11 in China, interpreted as moderate polygyny. Since these are historical averages and polygyny has been low recently, the model implies higher values for the past. Finally, Raisteiro and Chikhi (2013) focused on

² Non-recombining DNA segments (Omoto & Lurquin, 2004) contain genetic information that remains unchanged during the process of meiosis (cell division leading to the formation of eggs and sperm cells). In meiosis, data from paternal and maternal chromosomes can be swapped, resulting in new combinations of genetic information in the gametes. Non-recombining DNA is found on the Y chromosome (that only males have and pass on) and in the mitochondrion (the organelles of cells the genetic material of which is only inherited from the mother). Consequently, any change in those genes can only result from mutations and observing how these mutations spread in populations allows for the reconstruction of male and female lineages.

Europe and found genetic evidence of the spread of Neolithic farmers at the cost of ancient hunter-gatherers. They also observed some difference in male and female population growth, respectively. They suggest two, probably complementary, explanations: changes in females' residence after marriage (shift to patrilocality); and a shift from polygyny to monogamy.

Toward a more realistic history of human sexual selection

The evidence surveyed in this section so far suggests that mate choice, and female choice in particular, probably played a much lesser role in sexual selection in human evolution than assumed by Miller and others, whereas male contest probably played the most important role. In particular, polygyny and arranged marriage (at least in the last 50,000 years) were salient factors. Note that the term "polygyny" is often used very loosely; it might describe any situation with a variance in male reproductive success. However, a high ratio of females to males in the effective population (and thus an uneven distribution of male reproductive rates) can result from a multiple-male/multiple-female type of structure (as in chimpanzees and bonobos), isolated polygynous families (as in gorillas), or a multi-family society where some males have more than one wives, some have one, and others have none (as in some human societies). Appreciating the fundamental differences between these scenarios is crucial (cf. Chapais, 2008). We have seen that three quarters of extant hunter-gatherers practiced some level of polygyny mixed with monogamy in the last century. This structure differs radically from the polygyny of gorillas: while gorilla families consisting of a single male and several females live independently of each other, each in its own territory, polygynous human families live in larger groups, which also includes monogamous families and bachelors. Obviously, human polygyny also

radically differs from chimpanzee society: although the male reproduction rates in chimps are unevenly distributed, this arises from a largely promiscuous mating pattern, in which some males get more mating opportunities by being higher on the dominance ladder or otherwise pulling off clever mating tactics. The human case also radically differs from the monogamy practiced by gibbons, where monogamous families do not form a higher level of social organization.

There are good reasons to believe that the dominant human mating pattern has involved a mixture of polygamy and monogamy for a long while. Almost all studies of human dimorphism as well as genetic models, reviewed above, are consistent with polygyny being widespread in human pre-history. A notable exception is the phylogenetic study conducted by Walker and colleagues (Walker, Hill, Flinn, & Ellsworth, 2011), which (in spite of the fact that 73.7% of all the hunter-gatherers in the last century practiced some degree of polygyny), did not predict polygyny as the ancestral condition before some modern humans left Africa. This might simply indicate that levels of polygyny 50,000 years ago were already as low as today (or perhaps even lower), without necessarily contradicting the prediction that polygyny had been significant in the Pleistocene in general. There is more ambiguity as to how much *promiscuity* was going on in ancestral societies. If females mate with several partners, various psychological, behavioral, physiological, and anatomical strategies in males (and counter-strategies in females) evolve to decide on whose offspring the female will eventually gestate (Shackelford & Goetz, 2007). Although there is hardly any consensus among scholars regarding the interpretation of the evidence (see above), perhaps it is safe to conclude that our ancestors were somewhat, but probably not extremely, promiscuous. In other words, archaic humans formed long-term mating bonds, but mating also took place (although not too often) outside of these bonds.

Without filling in all the details at this point, the conclusion emerges that the problem of “how to guard my wives” is an earlier and more fundamental problem of hominid sexual selection than the problem of “how to court (ladies).” Our conclusions concerning ancestral mating patterns also caution that empirical research on the religious support of monogamy in contemporary societies cannot be used as evidence when studying the role of religion in archaic human and hominid groups. Consequently, in the final part of this article I will articulate a hypothesis of the origin of religion in the context of male-male conflict rather than monogamous marriage and courtship.

Terrestrial life and mate-guarding

A major leap in hominin evolution occurred 1.8 million years ago when *Homo erectus* became adapted to life on the ground. The anatomical features of *Homo erectus* witness a fully terrestrial life, in contrast to the *habilines* that were in this respect more similar to the *australopithecenes* and spent most of their time in the trees. Living and sleeping on the ground resulted in a number of important cognitive changes (Coolidge, Wynn, Overmann, & Hicks, 2015; cf. Beaune, Coolidge, & Wynn, 2009). Arboreal life protects all contemporary apes from predators and certainly gave similar protection to the *australopithecenes* and *habilines*. Once on the ground, however, *Homo erectus* needed some other defense: Coolidge et al. suggest large group size or fire. Large group size seems a more straightforward development, further supported by the connection between increased group size and the emergence of social learning in other studies (van Schaik & Burkart, 2011). Developed social learning in *Homo erectus* has been concluded from the cognitive analysis of its technology. *Homo erectus* produced novel

tools with bilaterally symmetrical edges (so-called bifaces), which cognitive analysis and empirical studies linked to novel cognitive capacities in the domains of visual processing and social learning.

After moving to the ground, archaic humans expanded their territorial range (Antón & Swisher, III, 2004). The transition to terrestrial life, increased group size, and the expansion of territorial range also had direct implications for sexual selection. In terms of Puts' dimensionality model (see above), corroborated by data about various species, moving from arboreal to terrestrial life implies an increase in mating competition, since monopolizing mating partners becomes a more viable strategy. Increased territorial range has the same effect, making it easier to guard a group of females from competing males. The size of such groups is limited by the cost of guarding females and the risk of breaking into other groups (Brotherton & Komers, 2003).

Chapais (2008) undertook a comparative study of the evolution of hominid mating systems. After considering several alternatives, Chapais (2008, pp. 135–184) suggests that our ancestors inherited (from the common ancestor of the great apes and humans) a multiple-male/multiple-female (chimpanzee-like) mating system that eventually gave way to a multi-harem structure. Without following Chapais' discussion in detail, we can note that he rejects the hypothesis that independent (gorilla-like) family units could amalgamate into larger societies (containing monogamous or polygamous bonds). First, the possibility of such a transition is contradicted by the cladistic analysis of the evolution of mating systems in non-human primates. Second, increased tolerance toward other males in a gorilla-like system would primarily favor the group leader's sons and result in a chimpanzee-like (rather than multiple-family) group. Third, general resemblances between hominid and chimpanzee anatomy,

behavior, and lifestyle suggest similarities of their mating systems, as well. Another important point Chapais makes is the distinction between breeding and economic bonds. Again, the details are rather involved, but comparative evidence from nonhuman primates proves the existence of both monogamous and polygamous mating without paternal care (Brotherton & Komers, 2003; van Schaik & Kappeler, 2003). Because of the unusually high costs of maternity in humans, as well as the extended time of childhood dependence on parents, parental bonding in humans evolved into economic cooperation. Finally, monogamy emerged as a special case of polygyny.

The essential feature of the multi-harem system is that females forage in smaller groups that can be guarded by a single male (against other males). Groups can temporarily coalesce for different purposes, such as sleeping or travel. Combining these arguments, I suggest that the move to terrestrial life lead to the formation of large groups, which, in turn, became differentiated into polygynous units. A necessary by-product of this differentiation was the appearance of a number of bachelors. Although the connection between the transition to the multi-harem mating system and the transition to terrestrial lifestyle I make here is conjectural, it is made plausible by Puts' dimensionality model as well as observations about the role of spatial distribution in sexual selection in general. For the purposes of this article it is enough to establish that in all likelihood the transition to the multi-harem system followed the transition to terrestrial life.

The multi-harem system gave male-male competition a prominent role in sexual selection. As we have seen above, intra-sexual male competition in a polygynous system is an extremely powerful selective force. If males managed to break into harems or females sought extra-pair copulations, both male and female choice could take place. The success of such attempts, however, was probably limited in a social structure based

on mate guarding, which is confirmed by evidence about the limited level of promiscuity (see above). The difference between multiple-female, multiple-male groups, on the one hand, and single-male, multiple-female harems, on the other, is crucial. Miller used the former model in his sketch of a “Pleistocene” scenario of sexual selection based on courtship. In doing so he relied extensively on anatomical arguments (e.g., moderate sexual dimorphism and genitals suited for sperm competition) that have been refuted by Dixson’s minutious analysis. The trajectory supported by recent scholarship, that is, the move from multiple-male/multiple-female group to harem to monogamy, tells a different story.

Novel sleep patterns and the emergence of religion

As *Homo erectus* transitioned to fully terrestrial life, changes in social structure and mating strategies coincided with an equally revolutionary development in its sleep patterns. According to Coolidge et al. (2015), another important consequence of terrestrial life was better sleep. Interruptions due to the danger of falling from trees as well as various disruptions by wind and other weather conditions disappeared. Increased protection by a large group and a more advanced technology (see above on bifaces) contributed to the quality of sleep. Undisturbed sleep resulted in an increased proportion of REM (rapid-eye-movement) and slow-wave sleep phases. In the great apes, REM-phases account for about 7–15 percent of total sleep, while in modern humans this has increased to 25 percent. Drawing on empirical evidence from dream research, Coolidge and colleagues suggest that better sleep had profound consequences

for cognition, including threat simulation and priming in dreams, as well as enhanced creativity, and improved memory consolidation (Coolidge et al., 2015, pp. 184–186).

Dream studies indicate that dreams are almost always depictions of social interactions of the dreamer with dream characters (McNamara 2016, p. 15–17). Further, there is substantial difference between the dream characters appearing in REM and non-REM-related sleep (NREM-sleep), respectively (McNamara et al. 2005; McNamara 2016, pp. 17-21). While dreams in NREM-sleep typically depict friendly interactions with known characters, the characters in REM-sleep-dreams are typically antagonistic and the dreamer is involved in aggressive encounters with them, which are initiated either by the stranger or the dreamer. There are also intriguing gender differences in dream content with respect to social encounters. (a) First, aggressive encounters in dreams typically occur between the dreamer and unknown male figures. (b) Second, such unknown males occur in men's dreams more frequently than in women's dreams. (c) Third, the dreamer is more often the receiver of aggression than the aggressor, with male dreamers being aggressors in somewhat more dreams (40 percent) than female dreamers (33 percent). Finally, the aggressive interactions typically involve the dreamer defending something valuable, such as self, family, property, or abstract ideas.

Recently McNamara (2009, pp. 193–205; 2016) revived the classical argument that god and spirit concepts originate in dreams. Historically, dreams have played a central role in virtually all forms of religion (e.g., Dodds, 1951, pp. 102–134; Jędrej & Shaw, 1992; Kelly, Adams, & Davis, 2009; Tedlock, 2005). Many scholars of the nineteenth and early twentieth centuries proposed a connection between dreams and the origin of religion, with more recent contributions drawing on empirical evidence from dream research (Tedlock, 2005; McNamara 2016, pp. 28-33). McNamara combined experimental data about dreams with neuroscience to explain how REM- and NREM-

sleep were involved in the formation of religious concepts. In particular, McNamara (2016, pp. 95–121) suggested that dreams provided building blocks to conceptualize superhuman agents, such as ancestors, spirits, and gods. The process that gives rise to concepts of supernatural agents includes five steps, which can be summarized in the following way (McNamara, 2016, p. 98): “Dreams give rise to SAs by reducing agency in the dreamer and transferring it several times over to another dream character (typically a stranger) who takes on supernatural powers and becomes a god or demon.”

Religion is a complex phenomenon, which includes, among others, conceptual, experiential, emotional, behavioral, and institutional components. These aspects of religion probably developed gradually in dynamical interaction with each other over a very long time so that it is not meaningful to declare that religion appeared at one or another particular point of human evolution. The appearance of symbolic thought might be a reasonable criterion for speaking about human religion in a proper sense (Geertz, 2013; Bellah, 2011; Deacon & Cashman, 2010; Mithen, 1996). I will use the term “proto-religious traits” to talk about traits related to religion before the appearance of symbolic competence. In light of the foregoing discussion of social encounters in dreams, it is quite plausible that the increased frequency of encounters with both friendly and antagonistic agents in extended REM-sleep had proto-religious significance. One has to take into consideration that *Homo erectus* did not know the difference between fact and fiction, a cognitive ability that emerged only later in human evolution (see below). We can surmise that dreams were accepted as part of reality, even more so than in pre-industrial human societies. *Homo erectus* could rehearse the events of a dream, reproduce its circumstances, or attempt to win the support of characters that appeared in dreams. Due to the lack of evidence, it is impossible to arrive at a precise reconstruction of these elementary forms of religion. We must assume,

however, that once such experiences, cognitions, and behaviors appeared they did not remain isolated from other aspects of the life of *Homo erectus*. In the rest of this article I offer some speculative thoughts on the connection between REM-sleep, mate-guarding, and proto-religion.

Mate-guarding and religion: tentative suggestions

Thus far we have seen that with the transition to a terrestrial habitat, *Homo erectus* gained the ability of guarding access to females by rival males. This transition also allowed for the extension of REM sleep, which in turn enabled the emergence of proto-religious experiences. Can we say more about the possible cognitive and behavioral connections between these developments?

(1) First, as Coolidge et al. (2015) argued, dreams helped the individual by simulation and priming. Revonsuo and Valli (2000) presented empirical evidence of the *threat simulation theory*. The authors observed that most repetitive dream contents are based on threats in ancestral environments, such as pursuits, fights, and attacks. They suggested that the evolved biological function of dreaming is to rehearse threat perception and threat avoidance skills. According to Franklin and Zyphur (2005), dreaming in ancestral environments also served as a rehearsal mechanism for scenarios encountered in daily life, facilitating decision-making prior to the advent of language. During REM sleep, the ventromedial prefrontal cortex, amygdala, and anterior cingulate cortex are activated, which are thought to play a strong role in social and interpersonal decision-making and evaluations (Coolidge et al, 2015, p. 185, citing Gazzaniga, Ivry, & Mangun, 2014). In general, priming and simulation in dreams could

help *Homo erectus* thrive in different domains of life, such as hunting and social interactions. However, given the dominant role of male intra-sexual competition in evolution as established above, any priming or simulation that supported mate-guarding efforts may have had superior selective advantage. Encounters with antagonistic dream figures (based on either archaic dream contents or waking life) could prepare males to guard their harems more efficiently, by improving the perception of threats posed by other males, facilitating decision-making about the appropriate response, and improving fighting skills. Unfortunately, our means to reconstruct the dream contents of *Homo erectus* are limited. One of the possibilities is to look at ancient, cross-culturally attested dream patterns. For example, the abundance of mythological and folklore themes related to overcoming challenges and fighting off powerful enemies in order to gain access to mating partners fits in well with the scenario of mating competition, although this is not necessarily restricted to mate-guarding. The gender-specific tendencies of antagonistic encounters in REM-sleep are intriguing in this respect. As we have seen above, men encounter more antagonistic dream figures than do women, and the antagonistic figures are male rather than female. The dreams are often about protecting valuable things or persons. Keeping in mind the usual caveats, these observations dovetail nicely with the supposed function of dreams to rehearse mate-guarding scenarios.

(2) Second, dream experiences with favorable contents could boost self-confidence. This could include receiving assurance of the support of a powerful dream figure (such as a deceased group member), winning a contest, or successfully mating with a partner (from a competitor's harem). Cross-culturally consistent patterns of the positive effects of favorable dream experiences can be cited as indirect evidence of the archaic use of dreams (Kracke, 2012). In general, there is ample evidence of the role of

dreams as means of gaining favorable portents from superhuman agents (such as ancestors, spirits, gods) as well as impersonal powers (such as astrological constellations) concerning endeavors both in private and communal life (e.g., Bloch, 2005; Lewis, 1976; Young, 1999). Attributing sophisticated skills of dream interpretation to *Homo erectus* would be certainly anachronistic. It is entirely plausible, however, that the reassurance gained from a favorable dream could boost his confidence much the same way it has affected cognitively more sophisticated humans throughout history.

(3) Further, *Homo erectus* probably used ritual displays to signal psychological (as well as physical) superiority to decide conflicts between males without physical fight. Chimpanzees, for example, perform elaborate displays (of dominance), which have been considered as evolutionary forerunners of human rituals (e.g., Winkelman, 2010, pp. 233–242). Signals of male dominance are widespread across species and are governed by a well-understood economy: if a conflict can be decided without paying the costs of physical investment and potential injuries, both parties are better off. Both sexual ornaments that evolve by female choice and the signaling of fighting ability in a competition for mates can be seen as “costly signals:” they represent “handicaps” as discussed above, taxing males’ reproductive fitness by draining time and energy; consequently, they can be maintained only if they bring substantial gains in sexual selection. As Berglund et al. (1996) demonstrated, however, in species where males contribute only sperm to progeny, traits that signal fighting ability are more likely to be maintained than signals of male quality to females. Signals used in contests are honest because they are constantly tested in combat with other males (Berglund et al., 1996, p. 389). In sum, if ritual displays related to proto-religious experiences signaled

underlying psychological and physical advantages reliably, they were adaptive in winning conflicts that arose from mate-guarding and were retained in natural selection.

(4) Fourth, the negative effects of unfavorable dream contents could be alleviated by magic and ritual. Across cultures, dreams are believed to provide opportunities for malevolent superhuman agents to attack people (e.g., Cheyne, Rueffer, & Newby-Clark, 1999; Pyysiäinen, 2009, 75–94; Stephens, 2005; Wei, 2011, pp. 121–160). Further, people turn to magical protection, purification, or exorcism to counter the negative influence of harmful spirits all over the world (e.g., Chán, 2005; Gaster, 2005; Winkelman, 2010, pp. 183–230). Even at an early stage of cognitive evolution, *Homo erectus* could develop elementary magical rituals in response to negative dream contents, as means of fighting off harmful influences. In addition to protective measures, *Homo erectus* could also try to gain the support of antagonistic dream characters. This could be understood as a forerunner of sacrifice, including some exchange to gain the favor of powerful superhuman agents and preventing them from doing (further) damage. Any of these behavioral responses to negative dream experiences conveyed psychological advantages, providing a sense of control and removing or ameliorating the threat represented by the dreams. Such psychological benefits, in turn, helped individuals in intra-sexual competition. The success of such counter-measures is strengthened by the confidence vested into them, which lent elementary magical beliefs a selective advantage.

(5) Fifth, the increased group size of *Homo erectus* and the related boost in social cognitive abilities also implies a new level of warfare. In the ethnographic evidence of warfare among hunter-gatherers, the control of women is a high-ranking, if not the most important, cause of war (Gat, 2000). This principle is independent of the general debate on the frequency of war among archaic foragers: even the recent,

contested study by Fry and Söderberg (2013) that predicted extremely low rates of warfare among hunter-gatherers indicated conflict over women as a significant factor in lethal aggression. Puts' (2010, p. 163) suggestion that males among early humans formed coalitions to gain access to women in between-group competition is probable in light of the combined evidence on male competition, group size, and hunter-gatherer societies. For bachelors, inter-group conflict could offer a possibility of accessing females without the risk of being ostracized by in-group males. If dreams and behavior rooted in dreams were selected for in the intra-sexual mate competition of males as discussed above, they probably also factored into inter-group conflicts. Again, it is difficult to reconstruct collective ritual behavior without the cognitive abilities that are taken for granted in ritual studies. Rituals that increase morale by creating synchrony (McNeill, 1995; Wiltermuth & Heath, 2009) could enhance the efficiency of collective action in conflicts, and checking for hard-to-fake signals of solidarity (Bulbulia, 2004; Irons, 2001; Murray & Moore, 2009; Sosis, 2003) are good candidates. Once we have accounted for the origins of superhuman agents and their survival in evolution, the costly signaling theory of rituals can be understood as an explanation of a particular function of rituals, rather than a general theory of them.

(6) Beyond the transition to ground sleep, Coolidge et al. (2015) proposed two other major leaps in human evolution. The expansion of working memory in *Homo sapiens* about a hundred thousand years ago probably changed religious thought and behavior. We can identify at least three relevant developments (Coolidge et al., 2015, pp. 192–193): increased verbal fluency, recursive structures, and episodic simulation. At this point, humans must have been expressing religious ideas verbally for a while, which implies that cultural transmission (including selective and epidemiological processes) had shaped religion. Based on new, enhanced linguistic faculties and the

capability of contemplating fictional scenarios, religious narratives that we commonly call “myths” appeared. Further, the increased cognitive capacity of recursion lead to the concept of deities with boundless qualities (Czachesz, 2012). More advanced religious thought and expression, in turn, could support a system of arranged marriages, where powerful superhuman agents were seen as guarantors of compliance with marital agreements. Religion could reduce the costs of mate guarding in two different ways: first, arranged marriages reduced the frequency and intensity of violence in the competition for mating partners; second, religion produced signals of chastity in marital bonds, as suggested by some scholars previously (see above). Further, female relatives could play a formal or informal part in marital arrangements, as attested in the ethnographic evidence (Apostolou, 2007a). This would bring a form of female choice into play before the appearance of female mate choice in courtship. Groups that reduced internal violence evidently thrived better than other groups. Consequently, an enhanced form of religion could spread by the replacement of populations or cultural influence.

Let us consider the third cognitive leap briefly, which was due to the enlargement of the parietal lobe. Coolidge et al. (2015, pp. 193–198) mention this development after the extension of working memory but do not date it specifically. The related enhancements of visual and motoric abilities as well as the perfection of numerical and symbolic cognition and representation laid the foundations for religious art, among others. It is tempting to quote mate choice or female choice at this point as a driving force of artistic displays and religion, as suggested by previous scholarship. However, we are still faced with the problem that the ancestral marital system of *Homo sapiens* was arranged marriage rather than courtship. Moreover, as we have seen, females often prefer the very traits that also signal male dominance, especially when it comes to mating (rather than long-term bonding). Religious behavior and artifacts could

also be used as symbolic markers that facilitated broader tribal associations, further reducing violence (Richerson & Boyd, 2005, pp. 211–213).

Conclusion and future directions

Given that sexual selection is an extremely powerful mechanism of evolutionary change, it is very likely that it influenced the development of religion in one way or another in evolutionary history. When and how such influence occurred, however, is difficult to establish. It is reasonable to think that over hundreds of thousands of years of hominin evolution, different types of sexual selection interacted with different aspects of religion more than once.

In exploring the connection between sexual selection and religion, this article focused on a particular event in evolutionary history, that is, the move of *Homo erectus* to sleep on the ground 1.8 million years ago because it brought about dramatic behavioral and cognitive changes that arguably resulted in the emergence of proto-religious concepts and behaviors. We combined theories about different aspects of human and hominid evolution to address the changes that occurred at that time and formulated the mate-guarding hypothesis of the origins of religion. (1) Based on his comparative work on the evolution of hominid mating patterns, Chapais concluded that our ancestors inherited a multiple-male/multiple-female (chimpanzee-like) mating system that eventually gave way to a multi-harem structure. (2) Drawing on Puts' dimensionality model and observations about the role of spatial distribution in sexual selection, we connected the transition to a multi-harem structure with the move to a fully terrestrial life. (3) We followed Coolidge et al. in analyzing the cognitive changes

brought about by the move to terrestrial life, highlighting the appearance of extended REM-sleep. Dreams in REM-sleep, according to Coolidge et al. and the literature they surveyed, functioned as threat simulation and preparation for waking-life scenarios. (4) Using the results of empirical dream research by McNamara and others, we emphasized the prevalence of antagonistic encounters in REM-sleep-dreams and the gender imbalance implying that males experience more of such dreams and the antagonistic dream figures are overwhelmingly males. (5) We discussed McNamara's suggestion that elements of superhuman agents in religion are derived from REM-sleep-dreams. Based on these insights from previous research, we proposed that proto-religious conceptualizations of superhuman agents and behavior connected to such concepts appeared in the context of REM-sleep-related dreams in *Homo erectus* about 1.8 million years ago and were selected for because they contributed to successful mate-guarding.

Finally, we can mention some possible future directions of research to test the ideas outlined above. Since polygyny was widespread until relatively recent times (in terms of evolutionary history), it is feasible to look for psychological and behavioral traits relevant to the mate-guarding hypothesis empirically. Let us consider some possibilities. First, the analysis of more historical and anthropological data can confirm the relationship between religion and intra-sexual male competition. Second, experimental dream research can shed more light on the connection between dream characters and superhuman agency. Third, the competitive advantage of strong religious or magical beliefs can be addressed. Fourth, previous experiments on religiosity and sexual stimuli can be adapted to find out whether the results are better explained by courtship or male competition.

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